THE HORSE *CORMOHIPPARION THEOBALDI* FROM THE NEOGENE OF PAKISTAN, WITH COMMENTS ON SIWALIK HIPPARIONS

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ABSTRACT. A well-preserved skull of a three-toed horse, which is one of only a few known from the Neogene Middle Siwaliks of the Potwar Plateau, Pakistan, is referred to *Cormohipparion theobaldi*. This conclusion is based on cranial, dental, and size criteria that are diagnostic of this genus and species and differentiate it from the small Siwalik hipparions. The Siwalik hipparions appear to represent a polyphyletic assemblage of at least two, and probably three, forms. As a result of recent field work it is suggested, in contrast to previous hypotheses, that the 'Hipparion Datum' involves more than one form. The Siwalik hipparions have phylogenetic affinities with two or more groups in Holarctica. *Cormohipparion theobaldi* appears most closely related to other species of this genus found in Clarendonian (late Miocene) deposits of North America.

THE Siwalik Hills of Pakistan and India have been one of the most important sources of Eurasian Neogene mammals for more than a century. This rich faunal sequence has attracted special attention because of the presence of early hominoid fossils, including *Ramapithecus* and *Sivapithecus* (Pilbeam *et al.* 1977*b*). During the last century, large collections of Siwalik mammals were made for the Geological Survey of India, Calcutta, and the British Museum (Natural History), London. These collections have been monographed by workers such as Falconer and Cautley (e.g. 1846–1849), Lydekker (e.g. 1880–1884), and Pilgrim (e.g. 1911, 1915, 1926, 1932). During the 1920s and 1930s, significant collections were made for the Yale Peabody Museum by G. Edward Lewis, and for the American Museum of Natural History by Barnum Brown (see Matthew 1929; Colbert 1935). Later collections were made by other institutions, including the Bavarian State Museum, Munich, and the Geological Institute, University of Utrecht. During this decade, extensive collections have been made by several groups including the Yale University–Geological Survey of Pakistan expedition (Pilbeam *et al.* 1977*a*). The Equidae, represented by hipparions and *Equus*, are of great abundance in the Siwaliks; they are second only to the Bovidae in number of specimens collected.

As is the case elsewhere with fossil horses, because of their cosmopolitan nature, the Siwalik hipparions are of great importance in establishing a framework for Holarctic biochronology and palaeozoogeography. Siwalik hipparions are mostly known from isolated teeth and postcranial elements. Therefore, it is not surprising that the taxonomy of these horses has traditionally been based on those elements. Skinner and MacFadden (1977, see discussion below) have recently shown that certain cranial characters can be used to sort out hipparions into several morphologically and phylogenetically distinctive groups. However, skulls of Siwalik hipparions are very rare and they have only been described in a few cases (e.g. Colbert 1935). The purpose of this report is to describe a well-preserved skull of *Cormohipparion theobaldi* from

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the Neogene Potwar Plateau of Pakistan and to interpret the phylogeny, biostratigraphy, and palaeozoogeography of Siwalik hipparions in the light of cranial and other characters.

The dental nomenclature used in this paper follows Stirton (1941), Skinner and Taylor (1967), and Skinner and MacFadden (1977).

The following specimen abbreviations are used in the text: AMNH: Department of Vertebrate Paleontology, the American Museum of Natural History, New York; GSI: Division of Palaeontology, Geological Survey of India, Calcutta; PUZ: University of the Punjab, Department of Zoology Collection, Lahore.

SYSTEMATICS OF SIWALIK HIPPARIONS

Only a synopsis of Siwalik hipparion systematics will be presented here, because this subject was recently reviewed elsewhere (Hussain 1971). Falconer and Cautley (1849) described the first species of Siwalik hipparion as *Hippotherium antilopinum*. Lydekker (1877) described a large species of *Hipparion* as *Sivalhippus theobaldi*. Subsequently three small species were described: *H. punjabiense* (Lydekker 1886), *H. perimense* (Pilgrim 1940), and *H. chisholmi* (Pilgrim 1910). Although in his taxonomy of *Hipparion* Colbert (1935) listed all five previously named species, he appears to support Matthew's (1929) idea of only two species, the large *H. theobaldi* and small *H. antilopinum* (including, in synonomy, the other three small species). Hussain (1971) follows the idea of two species in the Dhok Pathan Formation and, in addition, erects *H. nagriensis* for an intermediate-sized species that is restricted to the underlying Nagri Formation. These systematic discussions were largely based on analysis of isolated teeth and postcranial elements.

As a result of this traditional taxonomy of *Hipparion*, a total of several hundred species have to date been named from Holarctica and Africa. In some cases a new species is created out of despair because it is virtually impossible to fit one's local sample into a pre-existing species. Forstén (1968), in her revision of Old World hipparions, synonomizes the few hundred previously recognised species to thirteen, which are defined on dental and postcranial characters. This solution might appear to have alleviated the problems of unwieldy taxonomy; however, use of other characters such as cranial morphology suggests that Forstén's species may include polyphyletic or horizontal 'species' assemblages.

Skinner and MacFadden (1977) present a discussion of primarily North American hipparions in which discrete morphological groups at the generic level are based on cranial characters. Of particular relevance to the present discussion, one hipparion genus, *Cormohipparion*, is diagnosed by the presence of a preorbital facial fossa that is deeply pocketed posteriorly and has a relatively well-developed and usually continuous anterior rim (as well as a continuous posterior rim, but other hipparions also exhibit this character). It was also demonstrated that, based on analysis of three relatively large quarry samples ('populations') of *Cormohipparion*, the development of the preorbital facial fossa is of taxonomic value at the generic level, despite claims to the contrary. Besides *Cormohipparion*, several other discrete hipparion groups can be recognised by characters of cranial morphology. It would be satisfying from a practical point of view if cranial, dental, and postcranial characters could all be

used together to elucidate both generic and specific relationships. The present discussion is directed towards that goal.

SYSTEMATIC PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus CORMOHIPPARION Skinner and MacFadden, 1977
Cormohipparion theobaldi (Lydekker, 1877)

Text-fig. 1, Table 1

1877 *Sivalhippus theobaldi* Lydekker, pp. 31–32 (*nomen oblitum*).
1882 *Hippotherium theobaldi* Lydekker, pp. 81–87, pl. 11, figs. 3, 4; pl. 12, figs. 2, 4; pl. 13, figs. 1–3.
1885 *Hipparion theobaldi* Lydekker, pp. 58–60.
1929 *Hipparion theobaldi* Matthew, pp. 461, 524–526.
1935 *Hipparion theobaldi* Colbert, pp. 133–160, figs. 60–62, 64–70.
1968 '*Hipparion theobaldi*' Forstén, pp. 83, 87, 88, fig. 34.
1971 *Hipparion theobaldi* Hussain, pp. 37–47, 51–63, pl. 1, figs. 7–10; pl. 2, figs. 7, 8; pl. 3, figs. 1–3; pl. 4, figs. 1, 2; text-fig. 18*a*, *b*.
1977 *Cormohipparion* sp. Skinner and MacFadden, pp. 923, 924; text-fig. 7. (Selected synonomy, see Hussain 1971, for other references.)

Holotype. GSI C153, left maxillary fragment with dP^2–dP^4, from the Middle Siwaliks of the Potwar Plateau, Pakistan, see Lydekker (1882), pl. 11, fig. 4.

Revised diagnosis. Large and robust hipparion. Well-developed preorbital facial fossa that usually has a continuous anterior rim and is pocketed posteriorly. Upper cheek teeth large with thick cement, relatively complex enamel plications (especially on the posterior border of the prefossette and anterior border of the postfossette), plicaballin usually consists of two loops, and protocone oval to bean-shaped. Lower cheek teeth with deep ectoflexids in both the premolars and molars, and widely separated metaconids and metastylids. Robust tridactyl metapodials.

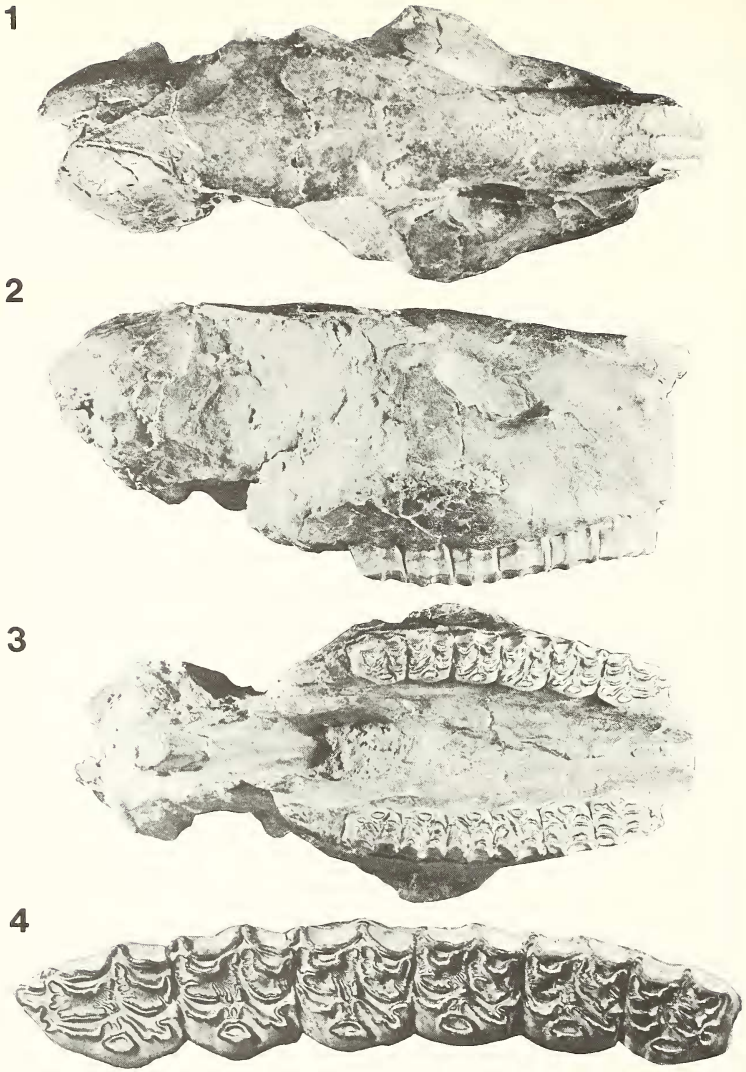
Referred specimen. PUZ 69/371, skull with facial, palatal, and dorsal occipital regions, and left and right P^2–M^3.

Occurrence. Collected by Professor A. Bakr and field party in 1969 from PUZ locality 45 near the village of Lehri (Middle Siwaliks, Dhok Pathan 'faunal stage'), Potwar Plateau, Pakistan (additional data are on file in the Department of Zoology, University of the Punjab, Lahore).

Description. PUZ 69/371 is a relatively well-preserved skull of a mature individual (text-fig. 1). The skull is not significantly crushed and the diagnostic generic and specific characters are preserved.

The buccinator fossa is anterior to P^2. The premaxillary–maxillary suture extends posteriorly to above P^2. The infraorbital foramen lies above P^3 anteroventral to the preorbital facial fossa. The preorbital facial fossa, which is developed on the nasal and maxillary bones, is relatively large (right antero-posterior length = 62 mm; right dorso-ventral width = 50 mm; left antero-posterior length = 64 mm; left dorso-ventral width = 46 mm; accuracy $\pm$ 5 mm) and lies above P^3–M^1. This fossa, with well-developed anterior and posterior rims and deep posterior pocket, is the principal diagnostic character of *Cormohipparion*. Although the sutures are difficult to distinguish, it appears that the lacrimal is triangular and lies posteroventral to the fossa. The anterior (maxillary) portion of the malar crest is moderately developed and the posterior (jugal) portion is not preserved. On the dorsal occipital region there are bilaterally symmetrical parietal crests that converge posteriorly. The posterior portion of the occipital region is not preserved and an endocast of sediment is exposed.

A complete set of the cheek tooth dentition (right and left P^2–M^3) is preserved. These teeth are large with relatively thick cement (Table 1). There is a progressive reduction posteriorly of the occlusal area of each tooth, i.e. P^2 is largest and M^3 is smallest.



TEXT-FIG. 1. *Cormohipparion theobaldi*, PUZ 69/371, from the Neogene Middle Siwaliks of Pakistan. 1, dorsal view of skull, $\times \frac{1}{3}$; 2, right lateral view of skull, $\times \frac{1}{3}$; 3, ventral view of skull, $\times \frac{1}{3}$; 4, occlusal view of left upper cheek teeth, $\times \frac{2}{3}$.

TABLE 1. Dental measurements (mm) of *Cormohipparion theobaldi*, PUZ 69/371.

Left side:	M^3	M^2	M^1	P^4	P^3	P^2
Greatest antero-posterior length	26·5	23·4	23·4	26·1	27·7	34·4
Greatest transverse width	22·2	24·8	26·5	29·6	29·5	27·8
Right Side:						
Greatest antero-posterior length	26·2	23·9	23·1	27·3	27·8	35·1
Greatest transverse width	22·1	26·0	27·0	29·1	29·0	29·0

The P^2 is triangular with a characteristically well-developed anterior extension of the parastyle. P^3–M^3 are roughly square. The parastyles and mesostyles are well-developed; the metastyles are weak. The prefossettes and postfossettes are richly plicated, with the maximum enamel folding on the posterior border of the prefossette and anterior border of the postfossette. The protolophs and metalophs are crescent shaped. The plicaballin consists of two principal folds on each tooth. The protocone is oval or bean shaped and it is characteristically isolated from the protoloph. The hypocone is not separated anteriorly from the metaloph (as is the case in some other equids where a postprotoconal groove separates the metaloph and hypocone). Posteriorly, the hypocone is separated from the metaloph by a moderately developed hypoconal groove.

Discussion. In his review of Siwalik hipparions, Hussain (1971) recognized three species. *Hipparion nagriensis* was characterized as being restricted to the Nagri Formation and of intermediate size relative to the two other species. *H. theobaldi*, found in the Dhok Pathan and Tatrot (Upper Siwaliks) Formations, was characterized by its large size and relatively robust metapodials. *H. antilopinum*, found contemporaneously with *H. theobaldi*, was characterized by its small size and relatively gracile metapodials.

It is evident from the present study that, based on the configuration of the preorbital facial fossa, the large species *theobaldi* can be assigned to the genus *Cormohipparion*. There are few other skulls of *Cormohipparion* from the Siwaliks known or described; as well as PUZ 69/371, similar facial configurations are illustrated for AMNH 19466 (Colbert 1935, p. 143, fig. 64) and AMNH 98728 (Skinner and MacFadden 1977, p. 923, fig. 7*a*). There are also dental characters that can be used to diagnose *C. theobaldi*. Certainly its large size has been noted by workers for more than a century. Present work in progress (MacFadden, in preparation) suggests that, besides size, there are distinctive differences in dental pattern. For example, in the upper cheek teeth, the plications on the posterior border of the prefossette and anterior border of the postfossette are more complex than in other Siwalik hipparions. Also, the plicaballin is more complex. In the lower cheek teeth the ectoflexids (external valleys) are very deep in both the premolars and molars. Correlated with the deep ectoflexids is the formation of a divided isthmus (including antero- and post-isthmus) and plicaballinid that is poorly developed or absent. In the smaller Siwalik hipparions, which we will refer to as the 'Small Hipparion Complex' (including *H. antilopinum s.s.* and *H. nagriensis*), the deep ectoflexids and correlated characters are also found in the molars. However, in contrast to *C. theobaldi*, there are usually shallow ectoflexids and prominent plicaballinids in the premolars. In summary, *C. theobaldi* can be set apart from the Small Hipparion Complex by characters including configuration of preorbital facial fossa, size, and dental pattern.

The Small Hipparion Complex is at present more difficult to diagnose on a combination of cranial, size, and dental characters. Within this complex there are at least

two cranial forms (phena), or species, belonging to two genera. The first group includes the skull described by Colbert (1935, p. 142, fig. 63), AMNH 19761, incorrectly referred to *Cormohipparion* by Skinner and MacFadden (1977, p. 923, figs. 7*b* and 7*c*). It now appears that AMNH 19761 should be considered a different form because of its significantly smaller preorbital facial fossa (even taking into consideration the small size of this skull). The taxonomic assignment of skulls exemplified by AMNH 19761 (and other specimens referred to *H. antilopinum* in Hussain 1971) is at present left as 'Small Hipparion Complex, *incertae sedis*'. It would be satisfying if all the small Siwalik hipparions had a facial morphology similar to AMNH 19761; if this were so, we could conclude that two genera and species are represented in the Siwaliks, *C. theobaldi* and '*H.*' *antilopinum*. However, it does not appear that all skulls of the Small Hipparion Complex are of a similar morphology. One specimen, GSI C349, from the Middle Siwaliks of Perim Island, India, is morphologically different from the Small Hipparion Complex, *incertae sedis*. In GSI C349, the preorbital facial fossa has a complete and well-defined posterior rim and pocket, but anteriorly the fossa is poorly defined and blends into the facial region. This configuration is most similar to that of forms such as *Hipparion s.s.* from the type locality of this genus, Mt. Léberon, France. Unfortunately, there are no other characters, such as size or pattern of the dentitions, that can also serve to separate the forms within the Small Hipparion Complex. This is not surprising, as a similar problem exists for western Eurasian hipparions, where Forstén (1968) has included in her earliest (Vallesian) species, *H. primigenius*, an assemblage that cannot be distinguished solely upon dental or size criteria, but is certainly polyphyletic if viewed in light of differences in cranial morphology.

In summary, the Siwalik hipparions are provisionally allocated to the following categories, based on cranial morphology, size differences, and dental pattern.

1. *Cormohipparion theobaldi*; well-developed preorbital facial fossa with complete anterior rim, deep pocket posteriorly, large size, complex plications and plicaballin in upper cheek teeth, deep ectoflexids in both the lower premolars and molars, robust metapodials (exemplified by PUZ 69/371).

2. Small Hipparion Complex (*antilopinum*-like); at least two skull forms, small size, plications less complex than *C. theobaldi*, lower molars with deep ectoflexids but lower premolars with shallow ectoflexids and well-developed plicaballinids. Metapodials relatively gracile.

a. Small Hipparion Complex, *incertae sedis*; significantly smaller preorbital facial fossa relative to *C. theobaldi* (exemplified by AMNH 19761).

b. *Hipparion*, *sensu stricto*, preorbital facial fossa rimmed and pocketed posteriorly but anteriorly poorly defined and blending into the facial region (exemplified by GSI C349).

The biostratigraphy of Siwalik hipparions is important from the aspects of Holarctic correlation and palaeozoogeography. Earlier workers stated that hipparions first occurred in the Chinji Formation (Lower Siwaliks), became abundant in the Nagri and Dhok Pathan Formations (Middle Siwaliks), and persisted into the Tatrot Formation (Upper Siwaliks). Recent workers have rejected the idea that hipparions

occur in the Chinji Formation, and it now appears that hipparions first appear in the lower part of the Nagri Formation (Hussain 1971; Simons *et al.* 1971; Pilbeam *et al.* 1977*a*). This first occurrence, or 'datum plane' apparently represents dispersal of hipparions into the Indo-Pakistan subcontinent. The value of the Hipparion Datum Plane was recognized by earlier workers (e.g. Colbert 1935) to be an important event in Neogene Holarctic biochronology, assuming that dispersal occurred rapidly. This assumption of rapid dispersal could not be tested until the recent advent of absolute dating techniques. Berggren and Van Couvering (1974), using a combination of radiometric dates and marine-terrestrial correlations, stated that the Hipparion Datum in the western Old World occurred at about 12·5 mya. Redating of the critical Höwenegg site in the Hegau region at the fossiliferous horizon suggests that the Hipparion Datum in the western Old World is about 2 million years younger than the Berggren and Van Couvering date of 12·5 mya (Becker-Platen *et al.* 1977). In the Potwar Plateau of Pakistan there are as yet no radiometric dates from the Middle Siwaliks. Recent chronological investigations in this region have concentrated on independently dating the faunas by magnetic polarity stratigraphy. In the Siwaliks, the Hipparion Datum occurs about 100 m below a distinctive long zone of normal polarity interpreted to be magnetic Epoch 9 (Barndt *et al.* 1978). Therefore, the age limits for the Hipparion Datum range from a maximum of 11·47 mya (Epoch 10–Epoch 11 boundary) to a minimum of 10·21 mya (Epoch 10–Epoch 9 boundary). If an extrapolation is performed within Epoch 10, then the Hipparion Datum, because it is near the upper boundary limit, is probably closer to the 10·21 age (radiometric data from Watkins and Walker 1977).

These data may be interpreted in two different ways. If the date of about 12·5 mya is accepted for the Hipparion Datum in the western Old World, then it appears that hipparions were palaeogeographically isolated from the Indo-Pakistan subcontinent for about two million years. On the other hand, if the dates of about 10·5 mya are accepted for the Hipparion Datum in the western Old World, then the dispersal of hipparions throughout this region, the Siwaliks, and probably the rest of Eurasia was a geologically instantaneous event. This latter hypothesis seems preferable, pending further absolute dates in critical late Miocene Old World sequences.

In his phylogeny of Siwalik hipparions, Hussain (1971) states that one intermediate-sized species, *H. nagriensis*, was involved in the Hipparion Datum. He also hypothesized that both the smaller *H. antilopinum* and larger *H. theobaldi* were descended from *H. nagriensis*. Therefore, Hussain implies speciation of Siwalik hipparions *in situ*. Based on recent field work by the Yale University–Geological Survey of Pakistan expeditions, Hussain's phylogenetic and biostratigraphic hypotheses should be modified. Numerous Yale–GSP localities in the Nagri Formation yield two distinct size classes (small and large). This distribution appears to continue through the Dhok Pathan Formation and possibly into the Tatrot. As a result of this study, these two forms are assigned to *Cormohipparion theobaldi* and the Small Hipparion Complex. Furthermore, it appears that at least two hipparion genera are involved in the Hipparion Datum and that these forms diversified prior to dispersal into the Indo-Pakistan subcontinent. *C. theobaldi* appears closely related to forms such as *C. occidentale* in the Clarendonian (late Miocene) of North America (see Skinner and MacFadden 1977). This genus is last found in latest Clarendonian—early Hemphillian

sediments in North America, but with its occurrence throughout the Dhok Pathan Formation and possibly the Tatrot Formation, which are roughly equivalent to the Hemphillian and younger Blancan North American Land Mammal Ages, *Cormohipparion* appears to have persisted later in the Siwaliks than in North America. Within the Small Hipparion Complex in the Siwaliks, the affinities of one form, '*incertae sedis*' is at present not certain, whereas the other form appears closely related to *Hipparion sensu stricto* from the Turolian of Mt. Léberon, France.

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